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PERSPECTIVE

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miCROPe 2019 – emerging research priorities towards microbe-assisted crop production

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One sentence summary: For improving microbe-assisted crop production, considering ecological aspects for microbial inoculation and making better use of plant genetic determinants of beneficial plant-microbe interactions for plant breeding is key.

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ABSTRACT

The miCROPe 2019 symposium, which took place from 2 to 5 December 2019 in Vienna, Austria, has unified researchers and industry from around the world to discuss *opportunities, challenges and needs* of microbe-assisted crop production. There is broad consensus that microorganisms—with their abilities to alleviate biotic and abiotic stresses and to improve plant nutrition—offer countless opportunities to enhance plant productivity and to ameliorate agricultural sustainability. However, microbe-assisted cultivation approaches face challenges that need to be addressed before a breakthrough of such technologies can be expected. Following up on the miCROPe symposium and a linked satellite workshop on breeding for beneficial plant-microbe interactions, we carved out research priorities towards successful implementation of microbiome knowledge for modern agriculture. These include (i) to solve context dependency for microbial inoculation approaches and (ii) to identify the genetic determinants to allow breeding for beneficial plant-microbiome interactions. With the combination of emerging third generation sequencing technologies and new causal research approaches, we now stand at the crossroad of utilising microbe-assisted crop production as a reliable and sustainable agronomic practice.

Keywords: plant-microbiome interactions; microbial inoculation; plant genetics; plant breeding; GxExM; biocontrol

MICROORGANISMS—A SOLUTION TO MAINTAIN YIELDS WITH REDUCED INPUTS

Global food production has almost doubled in the past 50 years and the increased yields are mainly due to high inputs of fertilisers, pesticides and water, selected crop varieties and

other technologies of the ‘Green Revolution’ (Tilman *et al.* 2002). However, this improvement has contributed to a range of environmental problems, such as the eutrophication of surface and ground water, reduced above- and below-ground biodiversity and global warming (Vitousek *et al.* 1997). Moreover, the

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production of mineral fertilisers (e.g. N) is highly energy demanding (Sutton et al. 2013), and fertiliser resources (e.g. P) will become more scarce in the near future (Cordell, Drangert and White 2009). There is an urgent need for more sustainable agricultural production and to reduce the carbon footprint of primary production. Microbial or microbiome-based approaches may substantially contribute to secure a more sustainable primary production as well as to assure food quality. The 'Green Revolution' has optimised plant growth and agricultural productivity and, besides the environmental concerns, further yield increases by agrochemical inputs are unlikely (Mann 1999). Instead, we need to re-gauge our aims and work towards yield stability by capitalising on beneficial microorganisms and microbiomes and thereby reducing the need of agrochemical inputs (Fig. 1A).

There are countless examples of individual plant-associated microorganisms that improve plant nutrition or enhance resistance to biotic or abiotic stresses (for more details see Parniske 2008; Lugtenberg and Kamilova 2009; Pieterse et al. 2014; Hardoim et al. 2015; Compant et al. 2019). Such microorganisms present promising opportunities to secure crop productivity and yield stability. However, in order to capitalise on their traits, we need to understand how to manage their ecological behaviour and functioning in plant and/or soil microbiomes (Schlaeppli and Bulgarelli 2015; Sessitsch, Pfaffenbichler and Mitter 2019). To enable microbe-assisted crop production, the agroecosystem can be managed (i) via 'microbes' (e.g. inoculation of beneficial microbes or their products), (ii) via 'plants' (e.g. plant genetics, intercropping or crop rotation) or (iii) via the 'soil' (e.g. organic amendments or no/reduced-tillage practices; Fig. 1B). While intercropping or crop rotation stand in focus of plant-based agroecosystem management (Garbeva et al. 2007; Song et al. 2007; Hauggaard-Nielsen et al. 2008; Jensen et al. 2015), the specific use of 'Plant Genetics' to support beneficial microbial interactions has received only little attention. In this perspective article, we focus on 'Microbial Inoculations' and 'Plant Genetics' as they were at the heart of the miCROPe symposium and for the practical aspects of agroecology and soil management we refer to specialised reviews (Stark et al. 2008; Bommarco, Kleijn and Potts 2013; Lemanceau et al. 2015; Bender, Wagg and van der Heijden 2016; Lori et al. 2017).

Researchers from academia and industry have met to further develop microbe-assisted crop production approaches and discuss opportunities, challenges and needs of this technology at the miCROPe symposium, which took place from 2 to 5 December 2019 in Vienna, Austria (www.micrope.org). Host genetics and seed treatments were specifically explored during the satellite workshop '2nd EUCARPIA Workshop on Implementing Plant-Microbe Interactions in Plant Breeding' (www.eucarpia.org). Here in this perspective article, we combine key messages from the symposium with our views and thoughts on emerging research priorities. We focus on the challenges of (i) successful applications of microorganisms for crop production and (ii) plant breeding towards improved interaction with beneficial microorganisms.

MICROBIAL INOCULATION

As microorganisms have the potential to promote stress resilience of plants, antagonise plant pathogens and have fertiliser effects, inoculation of selected microorganisms represents a promising approach to improve plant production (Sessitsch et al. 2018). Until the application of such beneficial microorganisms keeps its promise, a number of issues remain to be addressed for academia, industry as well as registration

authorities. The miCROPe symposium permitted the discourse between science and industry regarding regulation, registration, consumers and market forces for the commercial success of microbial inoculants. In particular, the needs for successful registration of biocontrol microorganisms were highlighted and guidelines were presented by Gianpiero Gueli Alletti (APIS Applied Insect Science, Germany) and Faina Kamilova (Knoell, Netherlands). At the miCROPe 2019, a broad range of impressive examples were shown and reminded us about the undoubted potential that microbial inoculations can be used for the suppression of pests, pathogens or weeds or for the alleviation of abiotic stresses. Below we highlight recent progress of a few particularly active research areas.

Particular progress was made to move beyond single strain applications. Various studies such as presented by Rafael da Souza (Campinas University, Brazil), Sylwia Jafra (Gdansk University, Poland) or Alejandro del Barrio-Duque (AIT, Austria) revealed new insights on the application of microbial consortia for biocontrol and biofertiliser applications (Correa de Souza et al. 2019; Del Barrio-Duque et al. 2019, 2020; Maciag et al. 2020). For instance, del Barrio Duque et al. (2019, 2020) revealed synergistic effects between fungal and bacterial strains to promote plant growth and to suppress root pathogens. In particular, the combination between *Serendipita indica*, a well-known plant beneficial fungus, and *Mycolicibacterium* strains, all isolated from plants, enhanced the growth-promoting effect of the fungus when tested on tomato plants. Also, the antagonistic effects against fungal pathogens such as *Rhizoctonia solani* and *Fusarium oxysporum* were enhanced (Del Barrio-Duque et al. 2019). A further example was presented by Klára Bradáčová (Hohenheim University, Germany) reporting synergistic effects of microbial consortia on nutrient acquisition (Bradacova et al. 2019). Furthermore, Jaderson Armanhi (Campinas University, Brazil) presented a novel screening platform to select microbial consortia improving drought tolerance (Correa de Souza et al. 2019) and Narges Moradtalab (Hohenheim University, Germany) selected microbial consortia able to improve cold tolerance of maize (Moradtalab et al. 2020).

Another area of notable progress in the field is research on the mechanistic understanding of beneficial plant-microbe interactions. Mechanistic understanding is also important from an application point of view as it is valuable e.g. for composing functionally complementary microbial consortia or for improving the expression of functional traits in the field, and it is equally important for obtaining registration approval. For instance, the role of microbial secondary metabolites for plant and soil health presented a highlight. Microbial secondary metabolites are well known to be important in beneficial plant-microbe interactions, e.g. for antagonising plant pathogens. One example are volatiles produced by microorganisms. They are known to serve for long-distance communication between microorganisms as well as for inducing systemic plant responses (Piechulla, Lemfack and Kai 2017; Tyc et al. 2017; Veselova, Plyuta and Khmel 2019). Paolina Garbeva (NIOO, Netherlands) showed that certain volatile organic compounds are exclusively produced when microbes were co-inoculated demonstrating the importance to increasingly consider microbial consortia and microbial interactions also for applications (Garbeva 2019). Another example, as permitted by genome and metagenome analyses, is the identification of beneficial microorganisms possessing certain plant growth-promoting characteristics as well as traits linked to production-relevant characteristics as shown by Rafael de Souza (Campinas University, Brazil) or Michael Ionesco (LavieBio, Israel; Correa de Souza et al. 2019; Ionescu 2019).

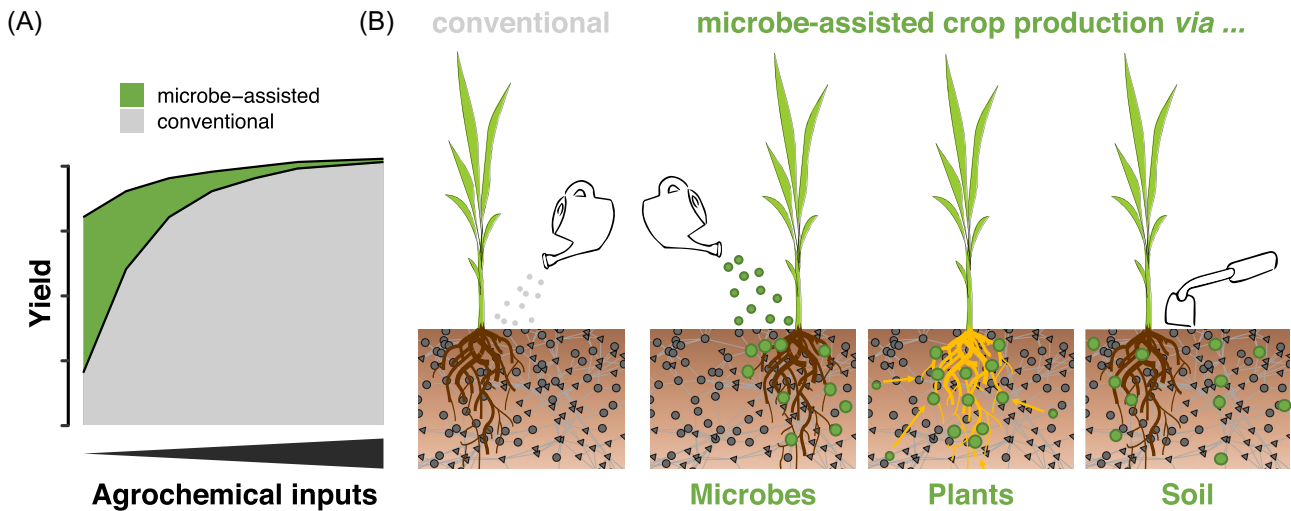


Figure 1. Approaches of microbe-assisted crop production | (A) Crop yields as a function of agrochemical inputs. Conventional crop production (grey) relies on agrochemical inputs such as fertilisers and pesticides. Microbe-assisted crop production (green) is designated to maintain yields but at reduced agrochemical inputs. (B) Conventional agriculture is compared to microbe-assisted crop production, where three players of the agroecosystem can be managed so that beneficial microbes (indicated as green dots) assist crop production. Beneficial microbes or their products are added to soil or plants/seeds (microbial inoculations). Specific plant species or cultivars recruit/enrich beneficial microorganisms from the surrounding soil. Dedicated soil management practices create conducive conditions for beneficial microbes.

Besides enhancing fundamental knowledge on the ecology of the introduced microorganisms and underlying mechanisms, there is also a need to improve the application technologies and suitable formulations to warrant high cell numbers and shelf-life (Mitter et al. 2019). Also novel approaches are needed (Peters 2019) as, for instance, Mohammadhossein Ravanbakhsh (Utrecht University, Netherlands) introduced the use of nanomaterials for phage treatment of bacterial wilt (Ravanbakhsh, Kowalchuk and Jousset 2019). A new application approach also includes soil transplantation, which was addressed by Jos Raaijmakers (NIOO, Netherlands). Furthermore, enhanced benefits of acclimatising individual microbes or entire communities to the target environment were reported, i.e. to pathogens (Ravanbakhsh, Kowalchuk and Jousset 2019), to heavy metals (Sabra et al. 2018) or to salinity stress (Dubey and Sharma 2019). The particular utility of the seed-associated microbiota was presented by Gabriele Berg (University of Technology Graz, Austria) and Matthieu Barret (INRAE, France; Adam et al. 2018; Torres-Cortes et al. 2018). The seed microbiota has only been explored for few years but represents a promising source of application-relevant microorganisms. As they may be in some cases transmitted to the next generation, flower application is a prominent mode to establish beneficial endophytes inside seeds (Mitter et al. 2017).

Taken together, a better understanding of the mechanisms and the ecology of potential inoculant strains or consortia will contribute to better design applications and make them more successful. We particularly lack understanding on the ecology of inoculated microorganisms under field conditions taking into consideration interactions with the resident microbiota as well as colonisation behaviour under different environmental conditions and with potentially different plant hosts or varieties. The variability of the inoculation response is a major issue—microbial inoculation may work in one environment but fail in another. To close this gap, we need to deepen our knowledge of the factors involved for successful colonisation or expression of the desired traits. Strain combinations or consortia combining microbial strains with complementary functions or synergistic interactions appear as a promising avenue. This avenue

is also followed by the industry. Another important criterion is inoculum dosage, which is tightly linked with the shelf-life of a microbial product or treated seed and the formulation in which a product is delivered. Alternative application approaches such as flower applications to yield inoculum-containing seeds (Mitter et al. 2017) open promising avenues as they have been shown to result in substantially improved colonisation behaviour. New formulation approaches considering nanomaterials or encapsulation have also shown potential to improve applications. Prediction models considering environmental conditions, plant genotype and the resident microbiome may lead to precision application of microorganisms in the future.

As a perspective, we see emerging a novel conceptual framework to enhance the success of microbial inoculation approaches. The undisputed impact of microorganisms on plant growth and health prompted Oyserman et al. (2019) to add the microbiome (M) as an explanatory factor to the basic model that a plant phenotype (Y) is determined by the relationship of genotype (G) x environment (E). Hence, the expanded model— $Y \sim G \times E \times M$ —explains plant yield as a function of the genotype, environment and microbiome interactions. We think that this GEM model conceptually also applies to microbial inoculation. The inoculation of a beneficial microorganism only successfully increases yield when all factors of the equation cooperate: G—the host plant genotype needs to be responsive to the inoculated microorganism(s), E—the inoculant needs to be adapted to the physicochemical soil environment and needs to establish in the local soil and/or plant microbiome (M). As further discussed below, there is tremendous genetic variation in host plants in their responsiveness to individual microbes or complex soil microbiomes as also highlighted at the miCROPe 2019 by e.g. Gwendolin Wehner, Adam Schikora (both Julius-Kühn Institute, Germany) and Klaus Schlaeppi (Basel University, Switzerland; Hu et al. 2018; Shrestha et al. 2019; Wehner et al. 2019a). It is very clear that not every plant variety will respond to a microbial inoculum, thus, we advocate for a careful evaluation of the host genotype (G) to assure successful microbial inoculation. With regard to the factor environment (E), it becomes more

and more evident that microbial inoculants should be adapted to the physicochemical soil environment. Microorganisms have well-defined growth requirements (e.g. pH), which explain their biogeography (Fierer 2017; Delgado-Baquerizo et al. 2018). We speculate that the microbial biogeography at least partly defines, for which condition(s) an inoculum will be suitable. Introducing unadapted microorganisms will inevitably fail to enhance plant yields. Ultimately, the inoculated microorganism needs to compete with the native microbiota (M) and this is an area that needs further research with the goal to understand which mechanisms underlie competitive abilities of microorganisms. Hence, we advocate that the full context dependency, encompassing host genotype (referring to G) as well as both the physicochemical (referring to E) and biological (referring to M) characteristics of a soil, requires careful evaluation to assure successful microbial inoculation. In summary, the GEM model presents a useful framework to solve the context dependency of microbial inoculations and, as such, gives the perspective of enhancing the predictability of microbe-assisted crop production.

PLANT GENETICS

Knowledge on plant genetic determinants for beneficial interactions with native soil microbiomes is growing rapidly. It has become clear that host genotype is not only relevant in the context of microbial inoculation (as discussed above) but plays also a significant role in driving microbial community composition and activity, selecting for and against particular members of the microbial community (Aira et al. 2010; Bulgarelli et al. 2015; Walters et al. 2018; Wille et al. 2019). There are a number of reports on host genotype influencing microbiome composition. However, in order to exploit genotype effects in breeding, we need to identify single loci that explain microbiome structure; as recent studies have shown (Lebeis 2015; Hu et al. 2018; Stringlis et al. 2018; Bulgarelli 2019; Zhang et al. 2019; Wehner et al. 2019b; Chen et al. 2020). The miCROPe symposium and the EUCARPIA satellite workshop aimed to reveal microbiome-based innovations by addressing the basic and applied aspects on mechanistic understanding of plant-microbiome interactions and the genetic potential of plant-microbiome responsiveness. Plant genetics of and breeding for beneficial plant-microbiome interactions were highlighted as underutilised and promising areas to improve crop resilience and yield stability. There have been fruitful and provoking discussions on the benefit of targeted microbiome-based genotype selections. While Jos Raaijmakers (NIOO, Netherlands) hypothesised that beneficial plant-associated microbiomes were indirectly co-selected throughout the history of breeding (Raaijmakers 2019), Richard Jefferson (Cambia & QUT, Australia) concluded that plant genome-focussed breeding has neglected agile trait contributions from the microbiome (Jefferson 2019). Matter-of-factly, comparing different genetic backgrounds, plant genotype was shown to play a small (~5% of variation) but significant role on microbiota composition (Hacquard et al. 2015).

Various studies revealed genotypic variation of plant responsiveness to microb(iom)es as revealed by genotype-dependent (i) colonisation success of mycorrhizal fungi (Schneider et al. 2019), (ii) recruitment of microbes under water and nutrient stress (Faist et al. 2019), (iii) microbe-mediated resistance by individual strains (Sefloo et al. 2019) or entire communities (Elhady et al. 2018), (iv) responsiveness to soil microbial feedbacks (Hu et al. 2018) and (v) bacterial quorum sensing molecules (Shrestha et al. 2019). Some studies unravelled mechanisms behind such genetic effects. For instance, genetic variation in responsiveness to microbe-induced priming involved stronger activation

of defence-related genes and cell wall structures (Shrestha et al. 2019). Other studies led to the discovery of quantitative trait loci (QTL) as a first step towards marker-assisted selection of microbiome responsiveness. Bulgarelli (2019) identified a QTL associated with the recruitment of specific members of the microbiome and Wehner et al. (2019b) reported the identification of a QTL for microbe-induced leaf rust resistance. Progress was also made for microbiome-based screening systems. For instance, Wille et al. (2020) demonstrated heritable variation for root rot resistance and significant correlations with field performance in a screening assay that involved the entire native soil microbiome as a key element of plant resistance. Other studies matched root morphological traits and the soil microbiome for enhanced nutrient and water uptake (Galindo-Castañeda, Hartmann and Lynch 2019) and growth, drought and cold tolerance (Orozovic et al. 2019) as a means to directly target plant-microbe interactions in breeding programmes. The group work session of the EUCARPIA workshop led to fruitful discussions on opportunities and challenges of implementing plant-microbe interactions in plant breeding. Opportunities were particularly seen in the area of yield stability (increased resilience for challenging conditions) and productivity (maintaining yield while reducing fossil-based inputs). Emphasised tools and applications were high-throughput phenotyping, machine learning and modelling approaches, novel seed treatments and the focus on endophytes, plant genetic markers, gene editing and monitoring and decision tools for agricultural practice and crop/genotype selection in general. The need to work closely with farmers and to link controlled experiments with field conditions was highlighted. Identified challenges involved the development of standards for -omics protocols, understanding of microbiome functions (beyond description), registration of microbial products and still unresolved problems with their performance variability.

In conclusion, to reach the goal to breed plants for improved interactions with microb(iom)es, the genetic understanding of the plant microbiome is a research priority. We are at the beginning of disentangling the principles that drive the observed phenotypic variation of different plant genotypes in their interaction with beneficial microorganisms or more generally with the native soil microbiota. The limited understanding of genotype-microbiome interactions is partly due to a lack of high-throughput screening tools available for selecting appropriate plant genotypes (Kroll, Agler and Kemen 2017; Walters et al. 2018; Beilsmith et al. 2019; Wille et al. 2019). A second challenge is the variability of soil microbiomes between different environments (E). Both the GEM model (Oyserman et al. 2019) and the focus on core microbiomes (Toju et al. 2018) present possible ways forward to solve the complexity of plant genotype (G) by soil microbiome (M) interactions. To implement microbiome-assisted crop production into practice, additional factors such as cultivation practices or 'soil management' (Fig. 1B) will refine the GEM model as framed earlier by Busby et al. (2017).

OUTLOOK

The miCROPe 2019 symposium as well as the EUCARPIA workshop bridged fundamental understanding of beneficial plant-microbiome interactions and the application of microbials or microbiome-based approaches for crop production. Conference and workshop presentations as well as multiple discussions between academia and industry led to the identification of new insights potentially leading to new innovations but also to the improvement of current approaches and applications. Overall, we conclude that a better understanding is particularly needed

on the functioning of soil and plant-associated microbiomes. Mechanistic insight exists mostly on a few isolated and well-studied microorganisms, however, such functional understanding is necessary for naturally-occurring and complex microbial communities in order to improve performance predictions. Furthermore, the interactions between the crop and its associated microbiome, or more generally the interactions within the holobiont, need further investigations. Ultimately, we need to link the beneficial functions of individual microorganisms or whole microbiomes with plant traits in order to (i) solve context dependency for microbial inoculation approaches and (ii) identify the genetic determinants to allow breeding for beneficial plant-microbiome interactions.

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